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NAMIB - Ornithology
ALAUDIDAE

WATER ECONOMY OF THE STARK'S LARK AND GREY-BACKED FINCH-LARK FROM THE NAMIB DESERT OF SOUTH WEST AFRICA*

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Abstract—1. Water budgets of two species of larks (Aves, Alaudidae), *Spizocorys starki* and *Eremopterix verticalis*, were determined from average measurements of pulmocutaneous evaporation rate, metabolic rate, excretory water loss and food consumption, at moderate ambient temperatures and humidities.

2. When air-dried millet seed was their only source of water, the birds' mean daily water loss exceeded water gain by about 0·6 g/bird; but water loss could be balanced against water gain by calculating the budgets with values of water loss from the lower end of the observed ranges of values.

3. Many individuals could survive indefinitely without drinking when consuming only millet seed.

4. The birds could not utilize NaCl solutions more concentrated than 0·30 M as drinking water.

5. The very low rates of evaporative and excretory water loss of these two species are adaptive to a dry environment.

INTRODUCTION

In recent years there has been considerable study of the physiological adaptations of birds to the hot, arid conditions of the desert (for reviews see Dawson & Schmidt-Nielsen, 1964; Schmidt-Nielsen, 1964). Most of these studies have been with North American desert species, and have led physiologists to the conclusion that with few exceptions desert birds do not have any special physiological adaptations for heat and aridity, but utilize physiological capacities which they share with non-desert species (Dawson & Schmidt-Nielsen, 1964, p. 490), and rely on various behavioral means of getting water and avoiding undue heat stress. However, this may not be so for birds inhabiting other, geologically older deserts of the world such as the Namib Desert of South West Africa, where birds may have had a longer time in which to evolve special adaptations to desert conditions (Bartholomew & Cade, 1963, pp. 529–531).

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The Namib is one of the driest, most barren deserts of the world (Logan, 1960), yet it is inhabited by a number of avian species including several species of larks, family Alaudidae (Willoughby & Cade, 1967). The purpose of this study was to gather data on the water metabolism of two small (16–18 g) seed-eating larks which are abundant in the Namib, the Stark's lark *Spizocorys starki* and the grey-backed finch-lark *Eremopterix verticalis*, to determine some of the ways by which they may have become physiologically adapted to the desert environment. These two species are of particular interest because their diets consist mostly of small seeds—the stomach contents of sixty-eight Stark's larks and fifty-five grey-backed finch-larks collected throughout the year contained 75 per cent and more than 90 per cent seed by volume, respectively. The rest of their food consisted of arthropods and small amounts of green vegetation. Thus these birds get very little preformed water in their food (around 10 per cent by weight of the seeds consumed plus the water in the small amounts of insects and green vegetation consumed). Also, field studies indicated that although many individuals drink when water is available, flocks of both species in the Namib range far away from sources of drinking water and appear seldom to need to drink (Willoughby & Cade, 1967). Thus, any physiological adjustments that reduce the water loss from the organism would be conducive to the survival of these species in the desert away from sources of drinking water.

MATERIALS AND METHODS

The field work and most of the laboratory work were done at the Namib Desert Research Station, Gobabeb (23° 34′ S., 15° 03′ E.; elevation 408 m), on the lower Kuiseb River about 60 miles southeast of Walvis Bay, South West Africa. Larks were captured in mist nets set up beside water holes where the birds came to drink. The birds were housed individually in small wire cages measuring 17·5 × 14·5 × 14·5 cm inside a small vivarium building. The floor of each cage had a layer of fine sand and a stone about 4 cm high for a perch. A shield of aluminium foil 7·5 cm wide surrounded the lower sides of the cage to prevent scattering of sand and seed outside the cage; and the bird could easily see over the top of the shield by standing on the stone. They were fed small-grained millet at all times, supplemented with occasional live mealworms (larvae of *Tenebrio molitor*). The food was simply scattered on the floor of the cage. Drinking water was supplied in a 60-ml graduated test-tube inverted over an L-shaped drinking spout with an outside diameter of 1 cm. The drinker was attached to the outside of the cage with the spout sticking into the cage.

Birds were successfully maintained in this manner for many months. The captives molted during the periods when wild birds did, and some of the Stark's larks sang vigorously inside their cages and even displayed toward others in neighbouring cages during the breeding period of wild birds.

Temperature and relative humidity

All birds were subjected to the normal photoperiod of Gobabeb, which varied not more than about 2½ hr during the year. Ambient temperature and humidity were not controlled, and followed those of the outside environment to some extent. During experiments, maximum and minimum temperatures in the vivarium were recorded daily, and relative humidity was recorded with a sling psychrometer in the morning between 08.00 and 10.00 hr and in the afternoon between 16.00 and 19.00 hr. The figures given for mean relative humidities during the experiments are actually means of the two daily readings during the particular experimental runs involved, and are therefore not true daily means of relative humidity. Nevertheless, I believe they can be considered reasonable approximations of the daily means.

Fluid consumption

When determining individual consumption rates of fluids, I fed birds only the air-dried millet, and read the water levels in the drinking devices to the nearest 0·5 ml at 1-, 2- or 3-day intervals in the late afternoon at about the same time of day. Evaporation from the drinking devices was monitored with an identical device mounted near the experimental cages. The amount of fluid lost by evaporation was routinely subtracted from the readings for the experimental birds. The mean daily fluid consumptions and attendant changes of body weight reported here are calculated from the results for 4–14 days, starting with the first day on which the birds were subjected to the experimental regimen. Each bird was maintained on tap water for at least 1 week before being subjected to the experimental regimen.

Both molting and non-molting birds were used for these measurements, but no differences were apparent in the performances of birds in the two conditions, so the data for the two were combined. Since birds in the wild spend about half the year molting (Willoughby, unpublished), it seems reasonable to combine data from the molting and non-molting birds. It is indicated in the results where data from molting birds were used.

Birds were weighed in the afternoon at the same time of day to keep track of changes in body weight. In this study, the term *initial body weight* means the body weight of the bird at the time it was first put onto the experimental regimen, and changes in body weight are calculated from weights taken subsequently at the same time of day.

Food consumption

Individual food consumption was determined by inserting the cage into a box that closely surrounded its lower half and had a 2·5 cm wide flange at the top turned inward toward the cage. This box caught all seed and excreta—using the term *excreta* to mean both urinary solids and feces—that were scattered by the activity of the bird. The metal floor of the cage was thoroughly cleaned before the bird was admitted, and the cage then was set into the box. A pre-weighed amount of seed was put into the cage, and 1 or 2 days later the uneaten seed and seed husks were poured out of the cage into the box, the bird was temporarily removed from the cage, and all the excreta adhering to parts of the cage were scraped off and added to the seed remainder. Any excreta voided by the bird while in the temporary holding cage were saved and added to the day's collection. The seed, husks and excreta were then collected into a shallow dish, the husks blown out of the dish, and the excreta separated from the seed by hand and saved. The remaining whole seed was weighed, and the difference between this weight and the initial weight was taken as the amount of whole seed consumed by the bird during the interval.

In these determinations birds were allowed to get used to the experimental conditions for 1 day before actual measurements of food consumption were begun. Only non-molting birds were used for these measurements.

Water content of excreta

Individual samples of excreta were picked off the cage floor with forceps within 5 sec of being voided and were quickly sealed in individual air-tight vials. A few minutes later they were weighed to the nearest 0·1 mg on a Mettler balance, then dried to a constant weight in an oven at 98–100°C. The difference between wet and dry weight gave the water content. All samples were taken from birds that appeared not to be frightened, but I did not attempt to hide from the birds' view when waiting for excreta to appear.

Birds that were deprived of drinking water normally produced only solid urine and feces of a putty-like consistency, so it was possible to collect whole samples with the forceps.

Evaporative water loss and metabolic rate

Evaporation rates and metabolic rates were determined during the daytime (10.00–17.00 hr) using a modified Haldane open-circuit gravimetric respirometer, with an aquarium air pump to provide air flow and $Mg(ClO_4)_2$ and flake NaOH in consecutive U-shaped drying tubes to absorb H_2O and CO_2, respectively. An additional U-tube of $Mg(ClO_4)_2$ was employed after the NaOH in both input and collection trains to check for any water released from the NaOH.

The respirometer chamber consisted of a glass desiccator with the bottom compartment filled with sunflower oil to trap excreta voided by the animal and to prevent their contributing water to the system. The air space inside the desiccator was 2 l., and an air flow rate through the chamber was maintained at 400 or 500 ml/min.

The bird was held in a small cage of $\frac{1}{4}$-in. mesh hardware cloth which was supported above the oil on a $\frac{1}{2}$-in. mesh wire platform. This small cage kept the bird within the air flow and away from the sides of the chamber. Evaporation data were discarded if droppings stuck to the wire. Air was admitted at the level of the platform via a plastic tube from the inlet at the top of the chamber and flowed out of the chamber at the top. Temperatures inside the chamber were monitored by a rapid-registering mercury thermometer inserted through the rubber stopper holding the air ducts.

Each subject was fasted for at least 4 hr before being put into the respirometer. The chamber was darkened by a double layer of black cloth covering it, and a period of at least 20 min with the air flow maintained at 400 or 500 ml/min was allowed for the bird to calm down and for the air in the chamber to reach satisfactory equilibrium, before the measurement was made. Carbon dioxide and H_2O were then collected from the air flowing out of the chamber over a period of 20 min, and determined by weighing the pick-up tubes before and after to the nearest 0·1 mg on a Mettler balance.

Relative humidities inside the chamber were calculated using the formula given by Lasiewski *et al.* (1966):

$$\text{percentage R.H.} = 100\,(x/y)/z,$$

where percentage R.H. is the percentage relative humidity; x, water vapor added to the dry air by the bird in mg/min; y, air flow rate in l/min; and z, density of saturated steam at the temperature of the chamber. In this calculation it is assumed that there is complete mixing of the air in the chamber.

At the air flow rates employed, air pressures inside the respirometer chamber averaged about 14 millibars above prevailing atmospheric pressure, measured by a small altimeter inside the chamber.

Body temperatures were taken with a rapid-registering mercury thermometer inserted 1–1·5 cm into the cloaca.

Only non-molting birds were used in the respirometry.

Calorimetry of food and excreta

Calorimetric determinations were done at Syracuse University with a Parr Instrument Company Plain Oxygen Bomb Calorimeter. It was assumed that the sulfur content of the burned samples was low enough to be neglected in calculations of heat equivalents of the samples. Caloric determinations on excreta were made from samples of the pooled collections from three individuals of each species.

RESULTS

Water deprivation

During the first water deprivation tests I noted in both species that the daily rate of weight loss was noticeably higher during the first 3 or 4 days of deprivation than during subsequent days, and I assumed that some physiological adjustments were being made by the birds during the initial period to reduce their rates of weight loss. In order to try to differentiate between the initial adjustment phase and the subsequent phase of the water deprivation response, I allowed birds to drink tap water during a period of 12 hr overnight beginning at the end of the fourth day and ending the next morning, and then observed weight changes when the birds were again deprived of drinking water.

The results of this experiment are presented in Fig. 1. Rates of weight loss for both species during the first 4 days of water deprivation averaged three or four times those during the subsequent 6 days, and clearly show that some kind of adjustment was made by the birds in response to water deprivation. In *E. verticalis* the mean daily weight loss for days 5–11 is statistically lower than for days 0–4 at $\alpha = 0{\cdot}01$ (single-tailed *t*-test), and in *S. starki* the second mean is statistically lower than the first at $\alpha = 0{\cdot}005$. Relative humidities during the first 4 days of deprivation, taken twice a day, averaged 38 per cent (range 24–57) and during the subsequent 7 days averaged 33 per cent (range 22–48).

One of the Stark's larks showed little or no change in rate of weight loss during water deprivation, and the values for this bird are connected by the dotted line in Fig. 1.

Figure 2 illustrates weight changes in four grey-backed finch-larks when deprived of water over a period of 30 days in September and October 1965. These examples are representative records for this species. None of these birds was molting. There was an initial steep drop in body weight, followed by a sharp reduction in the rate of weight loss on about the third or fourth day. Following this initial adjustment to water deprivation, all four birds showed some gain in weight, and presumably could maintain their body weight at the reduced levels indefinitely, although none was maintained on this regimen longer than 30 days. The mean relative humidity measured during this period was 41 per cent (range 13–71).

Figure 3 shows comparable data for weight change in four non-molting Stark's larks consuming only air-dried seed during May 1966. None of the Stark's larks was deprived of water for as long as the grey-backed finch-larks; but the data do show the ability of this species to check its weight loss and begin to gain weight within 15 days of water deprivation. The change from the initial rapid weight loss to little or no daily weight loss was not so clearly defined as for the grey-backed finch-lark, and this might be due to a slower adjustment. The main inflection in the curve of these Stark's larks occurred after the sixth day rather than after the fourth day as in the finch-larks. The mean relative humidity observed during this period was 25 per cent (range 14–38).

Drinking and utilization of NaCl solutions

The data for *ad libitum* consumption of distilled water and various concentrations of NaCl together with the observed changes of weight are presented in Figs. 4 and 5 for *E. verticalis* and *S. starki*, respectively. The periods during which these

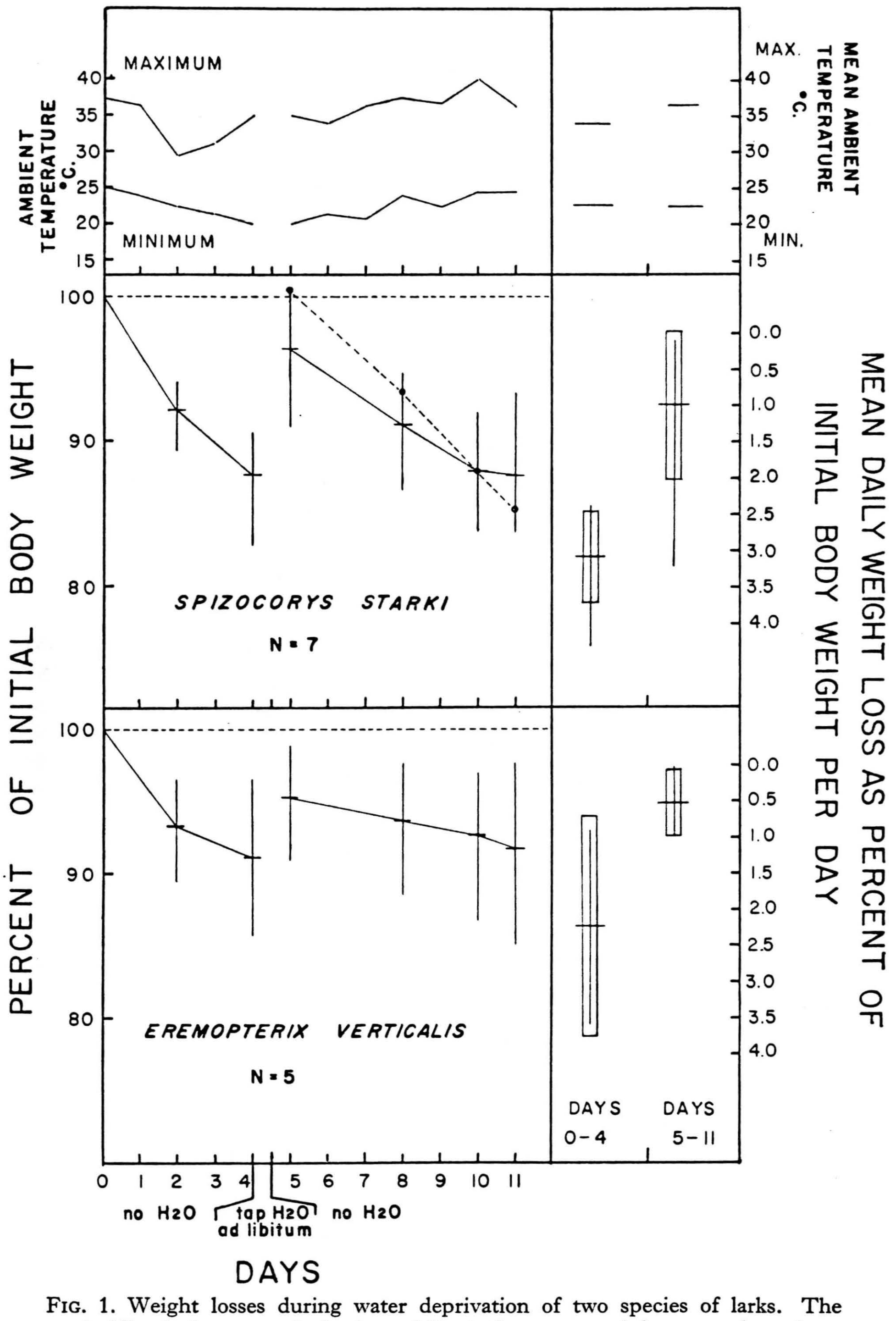

FIG. 1. Weight losses during water deprivation of two species of larks. The vertical line is the range; the horizontal line is the mean; and the rectangle encloses the 95 per cent confidence interval of the mean. The dotted line for *S. starki* during days 5–11 connects values of one individual that did not show a reduction in rate of weight loss.

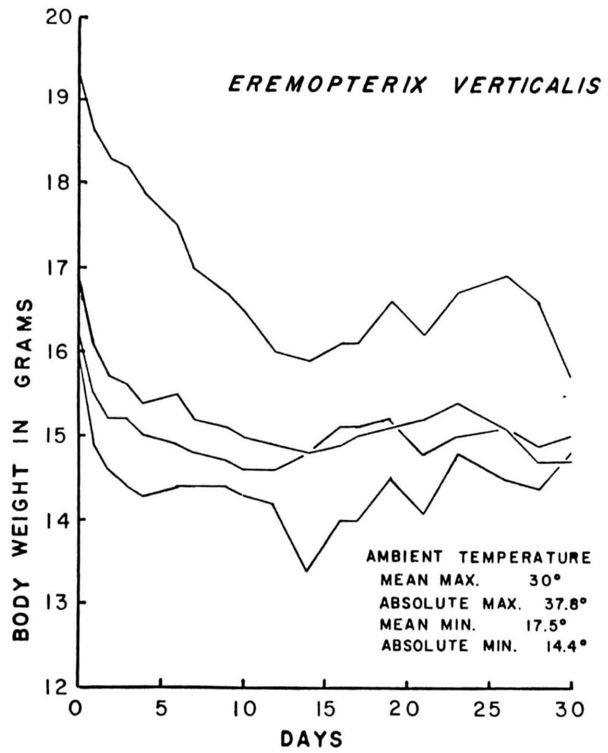

FIG. 2. Representative weight changes in *E. verticalis* consuming only air-dried seed.

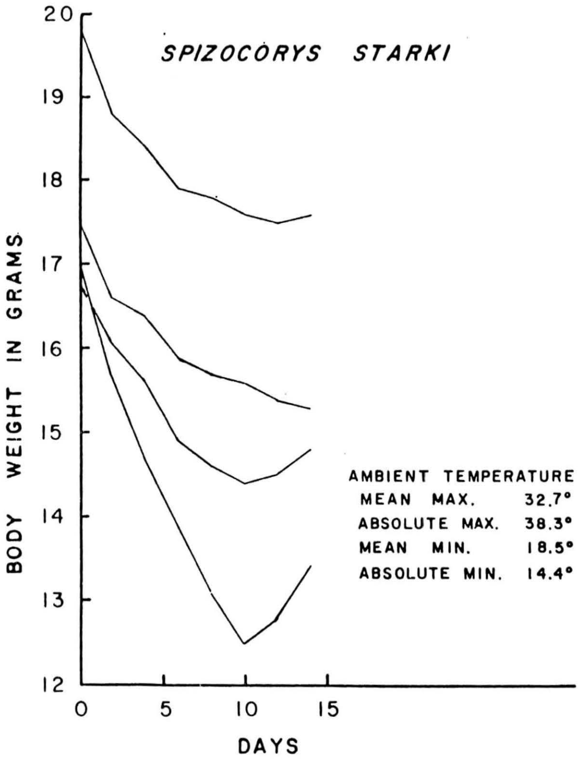

FIG. 3. Representative weight changes in *S. starki* consuming only air-dried seed.

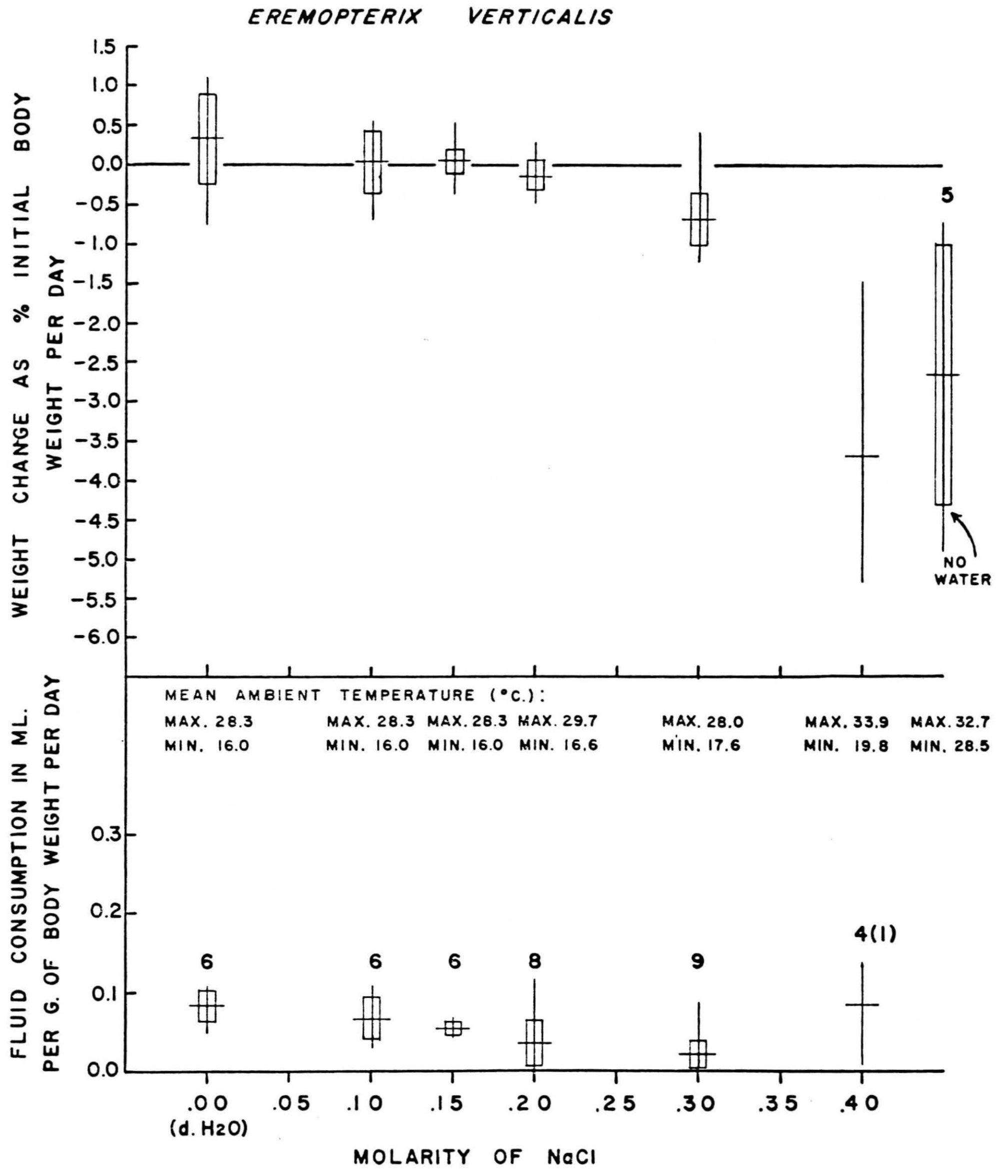

FIG. 4. Mean fluid consumptions and associated weight changes in *E. verticalis* drinking various NaCl concentrations. Vertical line is the range; horizontal line is the mean; the rectangle encloses the mean ±2 standard errors; numeral is the sample size (number of birds); numeral in parentheses is the number of birds in the sample that were molting.

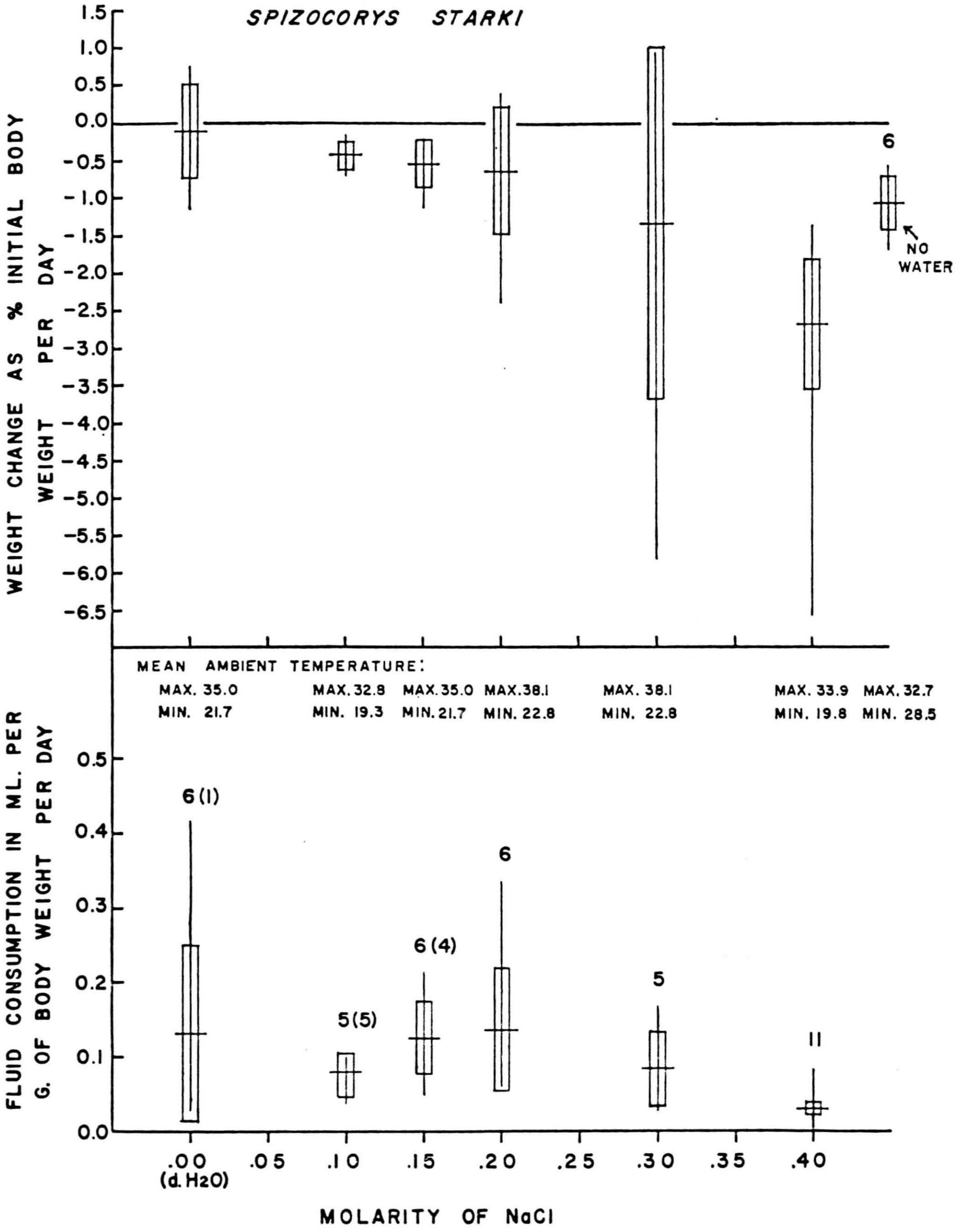

FIG. 5. Mean fluid consumption and associated weight changes in *S. starki* drinking various NaCl concentrations. Symbols as in Fig. 4.

measurements were made are given in Table 1. The precision of the measurements of fluid consumption was within 6 per cent when observations were taken at 5-day intervals.

TABLE 1—DATES OF MEASUREMENTS OF FLUID CONSUMPTION IN STARK'S LARK AND GREY-BACKED FINCH-LARK

	Period when measurements were made	
Regimen	*S. starki*	*E. verticalis*
Distilled H_2O	11–16 Jan.	22 Aug.–3 Sept.
0·10 M NaCl	27 Nov.–3 Dec.	22 Aug.–3 Sept.
0·15 M NaCl	11–16 Jan.	22 Aug.–3 Sept.
0·20 M NaCl	2–7 March	15–25 Sept.
0·30 M NaCl	2–7 March	29 Sept.–6 Oct.
0·40 M NaCl	18–22 April	18–22 April
No H_2O	9–23 May	9–23 May

Responses of both species to distilled H_2O, 0·10 M, 0·15 M, 0·20 M, 0·30 M and 0·40 M NaCl were not markedly different. *S. starki* showed considerably more variability in rates of consumption than did *E. verticalis*, but whether this has any significance is doubtful.

In both species, at least some individuals could maintain body weight on concentrations of NaCl up to 0·30 M, but none of them could maintain body weight on 0·40 M NaCl, and it may be concluded that 0·30 M NaCl is near the maximum concentration that any of these birds can utilize. Those drinking 0·40 M NaCl lost weight at the same rate or faster than those without any water to drink. Since these changes of weight were calculated from the first day on each regimen, the weights of non-drinking birds were not stable, as they might have been later, after becoming adjusted to water deprivation (Figs. 1, 2). Two of the five *E. verticalis* deprived of water for comparison with drinking birds (Fig. 4) died during the period of measurement—one died on the seventh and the other on the tenth day of water deprivation with rates of weight loss of 4·9 and 4·2 per cent of initial weight per day, respectively. Table 2 lists the observed relative humidities in each experimental period.

Respiratory metabolism

Carbon dioxide production and evaporative water loss were measured simultaneously at prevailing room temperatures for both species to compare the performance of birds that had been given water *ad libitum* with those that had been deprived of drinking water for 4 or 5 days. Such a comparison would show whether or not rates of evaporative water loss were reduced in response to water deprivation. Table 3 lists the calculated relative humidities in the respirometer chamber during these measurements, and Table 4 gives the body temperatures of birds taken immediately after the end of each metabolic measurement.

TABLE 2—MEAN PERCENTAGE RELATIVE HUMIDITIES OBSERVED DURING EXPERIMENTAL PERIODS, MEASURED TWICE DAILY

Regimen	*E. verticalis*	*S. starki*
Distilled H_2O	38·6	36·9
0·10 M NaCl	38·6	39·5
0·15 M NaCl	38·6	36·9
0·20 M NaCl	42·7	34·6
0·30 M NaCl	45·3	34·6
0·40 M NaCl	30·5	30·5
No H_2O	25·0	25·0

TABLE 3—CALCULATED PERCENTAGE RELATIVE HUMIDITIES IN RESPIROMETER CHAMBER DURING MEASUREMENTS OF RESPIRATORY METABOLISM, BASED ON RATES OF EVAPORATIVE WATER LOSS

	S. starki		*E. verticalis*	
	Watered	Water-deprived	Watered	Water-deprived
Mean	11·5	7·9	7·9	7·9
Range	6·8–15·7	4·0–18·0	4·3–14·7	3·6–19·3

Metabolic rates. No attempt was made to obtain a metabolic rate vs. ambient temperature curve, nor to compare the metabolic rate of one species with another because temperatures could not be controlled. Figures 6 and 7 present data on metabolic rate for *E. verticalis* and *S. starki*, respectively. The mean value for Stark's larks over a range of ambient temperatures 24–29·5°C, excluding one point at 25°C that falls well outside the cluster of values around that temperature, was 2·7 ml $CO_2/(g \times hr)$. If one assumes that the RQ was 0·71, this corresponds to a heat production of 6·7 kcal/day. The predicted standard metabolic rate for passerine birds of this size is 6·3 kcal/day, using the equation of Lasiewski & Dawson (1967): $MR = 129\ W^{0\cdot724}$, where MR is metabolic rate in kcal/day, and W is body weight in kg.

The mean value for metabolic rate in the grey-backed finch-larks over the temperature range 25–32°C is 2·8 ml $CO_2/(g \times hr)$, or, using the same conversion factors as above, is 6·7 kcal/day, compared to a predicted standard metabolic rate of 6·2 kcal/day.

I could detect no difference between the metabolic rates of watered birds and birds deprived of water, so the two groups were combined in each of the calculations of mean metabolic rate.

Evaporative water loss. Rates of evaporative water loss have been expressed both in terms of body weight and in terms of metabolic rate, because weight-relative evaporation rate in birds is related inversely to the body weight (Bartholomew & Dawson, 1953), and because evaporation rate is theoretically related directly to respiratory ventilation (Salt, 1964) which in turn should vary with metabolic demands.

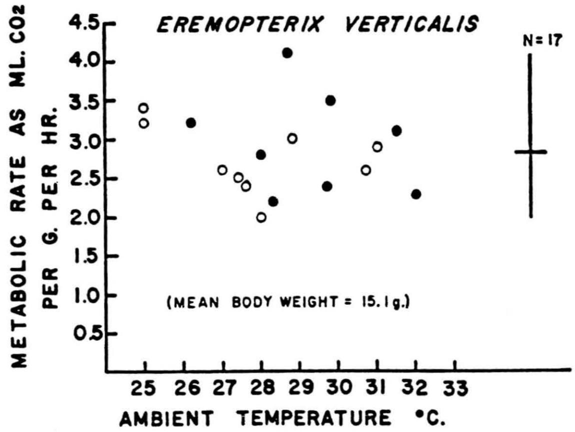

Fig. 6. Metabolic rate of *E. verticalis.* Open circles are values from birds deprived of water 4 or 5 days; blackened circles are values from watered birds. The vertical line is the range; and the horizontal line the mean.

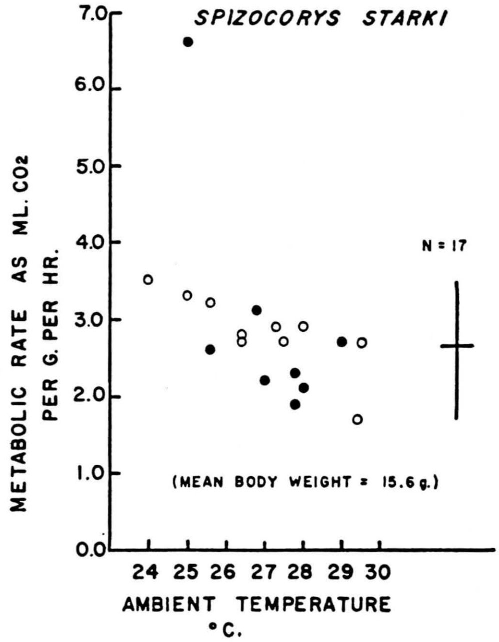

Fig. 7. Metabolic rate of *S. starki.* Symbols as in Fig. 6.

Figures 8 and 9 express data for water loss of *E. verticalis.* It is clear that the values for watered and unwatered birds do not differ significantly, and therefore that the water deprivation did not lead to a further reduction in rate of evaporation.

TABLE 4—BODY TEMPERATURES OF BIRDS TAKEN AT THE END OF RESPIRATORY METABOLISM MEASUREMENTS (°C)

	S. starki		*E. verticalis*	
	Watered	Water-deprived	Watered	Water-deprived
Mean	40·5	40·3	41·8	41·4
Range	39·0–41·5	38·0–41·5	40·4–42·5	40·0–42·5

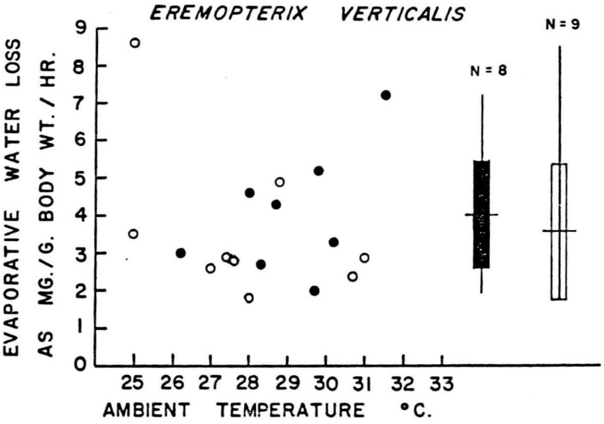

FIG. 8. Evaporative water loss in *E. verticalis* in relation to body weight. Open circles are values from birds deprived of water 4 or 5 days; blackened circles are from watered birds. The vertical line is the range, horizontal line the mean. The rectangle encloses the 95 per cent confidence interval of the mean. The blackened rectangle is for watered birds, open rectangle for unwatered birds.

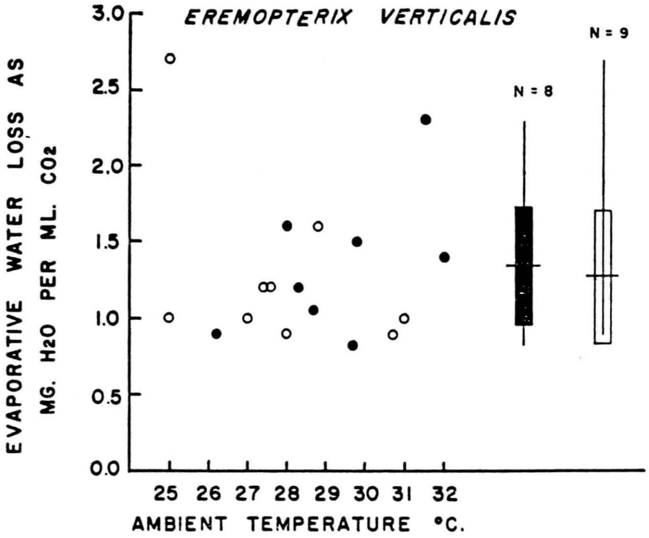

FIG. 9. Evaporative water loss in *E. verticalis* in relation to metabolic rate. Symbols as in Fig. 8.

Figures 10 and 11 show comparable data for *S. starki*. The mean evaporation rate in birds deprived of water was statistically lower than for watered birds at $\alpha = 0{\cdot}01$ when calculated with reference to metabolic rate, and at $\alpha = 0{\cdot}025$ when calculated with reference to body weight. The mean values for unwatered birds of both species are practically the same.

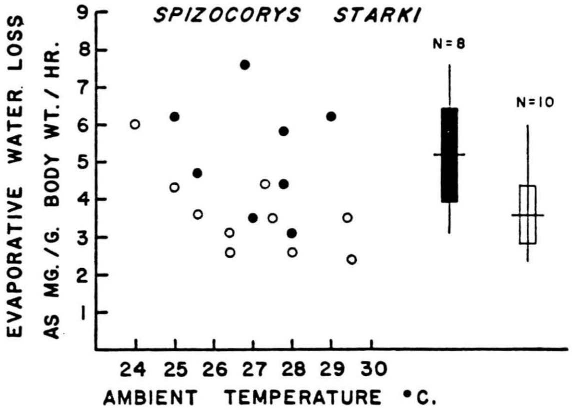

FIG. 10. Evaporative water loss in *S. starki* in relation to body weight. Symbols as in Fig. 8.

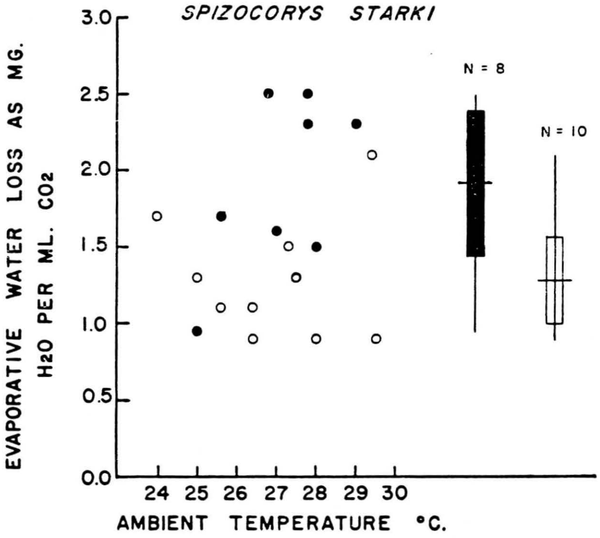

FIG. 11. Evaporative water loss in *S. starki* in relation to metabolic rate. Symbols as in Fig. 8.

Food consumption

Determination of the actual food consumption required measurement of the percentage of the whole seed consumed by the birds. Both species consistently cracked the husk from the seed, eating only the kernel. It was determined that this uneaten husk amounted to 12 per cent of the weight of the whole grain and had a lower caloric content than the kernel. Therefore, rates of food consumption expressed here are the values obtained in grams of whole seed consumed multiplied by 0·88.

Food consumption was measured in birds deprived of water and in those drinking water *ad libitum* (Table 5). The mean daily food consumption per bird in the unwatered grey-backed finch-larks was 81 per cent of the mean for watered birds, and in Stark's larks it was 60 per cent of the mean for watered birds.

TABLE 5—FOOD CONSUMPTION OF CAPTIVE GREY-BACKED FINCH-LARKS AND STARK'S LARKS (FOOD = SMALL MILLET SEED)

	E. verticalis		*S. starki*	
	Watered	Unwatered	Watered	Unwatered
Mean daily food consumption (g/bird)	2·20	1·78	1·90	1·13
Range	1·82–2·68	0·90–2·40	1·62–2·33	0·88–1·44
Number of birds	6	6	6	4
Mean initial body weight (g)	16·7	18·8	18·0	17·1
Mean daily weight loss as % initial body weight	0·6	2·6	1·0	3·5

Birds in all experimental groups experienced a net weight loss during the 5–6 days during which measurements were made, whether they had drinking water or not; but birds deprived of water on the average lost weight three or four times faster than did birds with water to drink.

Water content of excreta

The feces and urine are potentially critical avenues of water loss to any animal in a dry environment. Therefore it was necessary to determine how much water was lost in this way by these two larks in captivity. Samples were taken from both watered birds and from birds deprived of water for 4–9 days. Although watered birds frequently produced watery urine, only relatively dry, formed fecal and urine pellets were measured. I made no attempt to separate urinary and fecal components of these pellets. The water content in excreta was similar in both species (Fig. 12). Values in unwatered birds were as low as 30 per cent in *E. verticalis*, and 25 per cent in *S. starki*, but the mean of values was a little over 50 per cent.

Water content of food

The water content of the whole seed fed the birds throughout the experiments was 8·9 per cent. The uneaten husks contained 7·4 per cent water by weight, leaving the rest of the kernel with about 9·1 per cent.

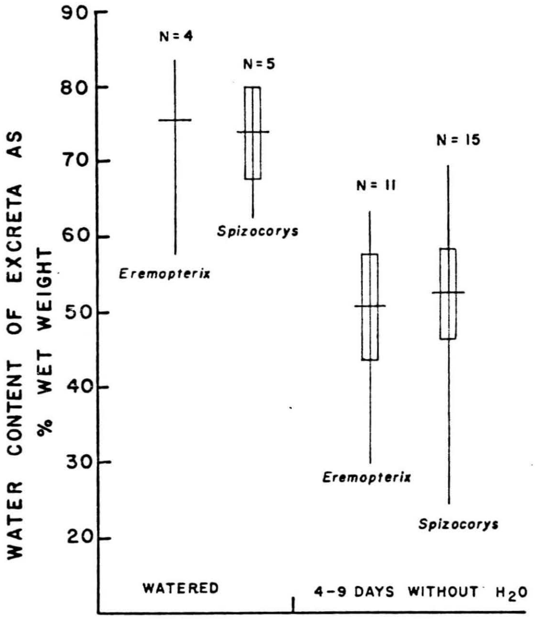

FIG. 12. Water content of excreta collected from watered and unwatered larks. The vertical line is the range; horizontal line is the mean; the rectangle encloses the mean ± 2 standard errors.

Caloric value of food and excreta

The mean caloric content of food, determined on two samples of husked seed, was 4·2 kcal/g. The mean caloric content of two samples of excreta each of water-deprived *S. starki* and *E. verticalis* was 3·8 kcal/g and 3·3 kcal/g, respectively.

TABLE 6—EXCRETA PRODUCTION IN CAPTIVE GREY-BACKED FINCH-LARKS AND STARK'S LARKS

	E. verticalis		*S. starki*	
	Watered	Unwatered	Watered	Unwatered
Mean daily excreta (g/bird)	0·29	0·26	0·34	0·20
Number of birds	5	5	6	4
Mean initial body weight (g)	16·5	18·5	18·0	17·1
g excreta/g seed eaten	0·132	0·146	0·178	0·177

DISCUSSION

Water deprivation

When initially deprived of water, the rate of weight loss by the larks was high, but in a few days body weight tended to stabilize and individuals even gained weight. The data in Fig. 1 illustrate this tendency, and rule out the possibility that the reduction in rate of weight loss after the initial 4 days of water deprivation was a result of lower ambient temperature and higher relative humidities, since during the second period (days 5–11) mean maximum temperature was higher and relative humidity lower than during the first period of deprivation.

Figures 4 and 5 include weight loss during 14 days of deprivation, and show that the five grey-backed finch-larks (Fig. 4) had a considerably higher rate of weight loss than did Stark's larks (Fig. 5). This was owing principally to the performances of the two finch-larks that died after rapid loss of weight during the experiment and is probably an example of sample bias.

Survival of some individuals for many days or weeks when deprived of drinking water is quite remarkable, but is now known in some other species of small desert birds. While most small birds lose weight steadily and die in 3 or 4 days when deprived of water and fed dry seed, it has been found that some individual budgerygahs *Melopsittacus undulatus* (Cade & Dybas, 1962), zebra finches *Taeniopygia castanotis* (Cade *et al.*, 1965), scaly feathered weavers *Sporopipes squamifrons* (Cade, 1965), black-throated sparrows *Amphispiza bilineata* (Smyth & Bartholomew, 1966), lark-like buntings *Fringillaria impetuani* (Willoughby & Cade, 1967), savannah sparrows *Passerculus sandwichensis rostratus* (Cade & Bartholomew, 1959), red-headed finches *Amadina erythrocephala* (Cade and Prozesky, personal communication), and violet-eared waxbills *Granatina granatina* (Cade and Prozesky, personal communication) can live indefinitely without a drink at moderate temperatures and humidities.

Drinking and utilization of NaCl solutions

The results show that both lark species have unusually low *ad libitum* consumptions of distilled water that actually fall below the predicted weight-relative rates of evaporation for birds of this size (Bartholomew & Cade, 1963, p. 508). *S. starki* consumed an average of 13 per cent of body weight per day, while *E. verticalis* consumed only about 8 per cent of body weight per day. *Ad libitum* consumption for most birds of this size range (18 g) exceeds 20 per cent of body weight per day (Bartholomew & Cade, 1963, p. 511).

The abilities of these two larks to utilize NaCl solutions for drinking water are not outstanding. Individuals could maintain body weight while drinking concentrations up to 0·30 M, but the tolerance limit for the majority fell somewhere between 0·20 and 0·30 M. This is slightly better than the upper limits of around 0·17 M found for the mourning dove *Zenaidura macroura* (Bartholomew & MacMillen, 1960), 0·15 M for the ground dove *Columbina passerina* (Willoughby, 1966), and about 0·15 M (25 per cent sea water) and about 0·23 M (37·5 per cent sea water) in the Inca dove *Scardafella inca* and white-winged dove *Zenaida asiatica*, respectively (MacMillen & Trost, 1966). It is about equal to the performance of the house finch *Carpodacus mexicanus* (Poulson & Bartholomew, 1962a), but far inferior to the abilities of some individuals of the zebra finch that can maintain body weight when drinking 0·6 M NaCl (Oksche *et al.*, 1963), and of salt-marsh-dwelling races of the savannah sparrow that can make use of NaCl concentrations up to 0·7 M and 100 per cent sea water (Cade & Bartholomew, 1959; Poulson & Bartholomew, 1962b). This means that these two larks probably do not have any extraordinary ability to excrete high concentrations of NaCl, and could not make use of very saline waters in the environment such as salt springs to obtain physiologically useful water.

Respiratory metabolism

Metabolic rates. The carbon dioxide production of these birds during the daytime at prevailing ambient temperatures indicated that metabolism was somewhat higher than that predicted for resting birds at thermal neutrality. This may be the result of measurements that were made outside the limits of thermal neutrality. Nevertheless, it appears that many of the values obtained do approach the predicted metabolic rate.

Evaporative water loss. The mean rates of evaporation were less than 9 per cent of body weight per day for both species after being deprived of water for 4 or 5 days. This is less than half the rate expected on the basis of measurements obtained from various small passerines (Bartholomew & Dawson, 1953; Bartholomew & Cade, 1963). Even the mean *ad libitum* consumption of both species was less than the predicted evaporation rate for birds of this body size, and indicates a definite adaptive reduction in pulmo-cutaneous water loss. In *S. starki*, water evaporated per ml CO_2 produced was significantly lower in birds deprived of water than in birds given water to drink. Therefore the birds must be effecting some adjustment to reduce evaporation from the surfaces of the respiratory tract, assuming that cutaneous evaporation is negligible. The mechanism of this reduced evaporation rate is not understood, but some hypotheses have been suggested.

One suggested mechanism for this reduction is that expired air might be cooled by varying degrees as it passed out through the trachea, in which case it would hold less water at saturation than if it left the bird's body at the temperature of the pulmonary surfaces (Cade *et al.*, 1965). The possibility that ventilation of the lungs and air sacs may be altered to change rates of evaporation has been suggested (Calder, 1964; Salt, 1964; Cade *et al.*, 1965), but the avian respiratory system is very complex (King, 1966) and the way in which this might occur is obscure. Another possibility is that the birds may somehow increase the amount of O_2 and CO_2 exchanged at each breath and thus reduce the total volume of air respired without necessarily altering ventilation pathways in lungs and air sacs.

Food consumption

The reduced food consumption by birds deprived of water compared to those drinking *ad libitum* (Table 5) may be owing partly to reduced activity in unwatered birds. However, it stems mainly from reduced feeding during the initial period of water deprivation. Richard Valle (personal communication) has observed a consistent reduction of food consumption in the budgerygah during the first 3 or 4 days of water deprivation, followed by a return to normal food consumption.

Water content of excreta

The water content of the excreta of these two larks deprived of water was remarkably low. Comparable mean values for excretory water content of small xerophilous species on restricted water intake that have been published are budgerygah, 68·1 per cent (Cade & Dybas, 1962); zebra finch, 65·3 per cent (Calder, 1964); and black-throated sparrow, 57 per cent (Smyth & Bartholomew, 1966).

Water budgets

Using the data presented above, it is possible to construct water budgets for both species to show how the birds can balance water loss against water gain without drinking. It is possible to calculate the budget starting directly with the observed metabolic rates, which would be likely to give a minimum value for metabolic water production. It is also possible to start with total metabolizable energy in the food, which would be likely to give a higher value for metabolic water production in each budget.

Table 7 shows the calculations of water budgets for both species under laboratory conditions by both methods, using mean values for metabolic rates, evaporation rates and rates of food consumption. Although the daily water deficit when calculated from total metabolizable energy in the food is slightly more favorable to the bird than when calculated from observed metabolic rate, it still exceeds 3 per cent of body weight per day, which is higher than that indicated in Fig. 1 by the weight loss of birds that had adjusted to water deprivation (days 5–11).

It is possible to bring the values for water loss and gain into closer agreement by using lower values for evaporative and excretory water loss. If for *S. starki* the evaporation rate is taken to be 2·6 mg/(g × hr), which is within the observed range of values, instead of 3·6 mg/(g × hr), and if the water content of the excreta is taken to be 35 per cent, which is also within the observed range of values, then the total daily water loss would be 1·17 g/day, leaving a deficit of only 0·08 g/day. Only a slight further reduction of water loss by either avenue in this case would be sufficient to balance the budget. In the case of *E. verticalis*, an evaporation rate of 2·0 mg/(g × hr) and excretory water content of 35 per cent result in a total water loss of only 0·90 g/day, leaving a slight surplus of water in the budget. In fact, evaporation rates measured in the respirometer probably were higher than at ordinary room conditions because relative humidity inside the chamber was considerably lower than that to which the birds were normally exposed. Therefore the birds were normally in a more favorable position to maintain water balance than has been accounted for in the calculations of Table 7.

Thus it is demonstrated that at least some individuals of these two larks can survive in moderate laboratory conditions without drinking, and so can a few other small xerophilous species, because they have very low rates of water loss. Whether they can survive in the wild without extra water is another question, because the need to evaporate water for cooling becomes an important problem. I have no data concerning thermoregulation in these two larks. On hot days in the field (air

TABLE 7—CALCULATION OF DAILY WATER BUDGETS FOR *S. starki* AND *E. verticalis* UNDER LABORATORY CONDITIONS

	S. starki	*E. verticalis*
Calculation using observed metabolic rates:		
Body weight	16 g	16 g
Metabolic rate	6·7 kcal/day	6·7 kcal/day
Caloric content of food	4·2 kcal/g	4·2 kcal/g
Caloric content of excreta	3·8 kcal/g	3·3 kcal/g
Water content of excreta	52%	51%
g excreta produced/g food eaten	0·18	0·14
Preformed water in food	9%	9%
Food composition (Bowes & Church, 1966, p. 114) (food = millet)	Protein	= 9·92%
	Fat	= 2·91%
	Carbohydrate	= 73·0%
g water produced/g protein oxidized	0·499	
g water produced/g fat oxidized	1·071	
g water produced/g carbohydrate oxidized	0·556	
Calculated food consumption	1·90 g/day	1·79 g/day
a. *Water gained:*	(g)	(g)
Preformed	0·17	0·16
Metabolic	0·93	0·85
Total	1·10	1·01
b. *Water lost:*		
Evaporation	1·38	1·38
Excreta	0·37	0·26
Total	1·75	1·64
a − b	−0·65	−0·63
Calculation using total metabolizable energy in food:		
Body weight	18 g (Table 5)	17 g (Table 5)
Food consumption of watered birds*	1·90 g/day	2·20 g/day
l. oxygen consumed/g carbohydrate oxidized	0·83	
l. oxygen consumed/g fat oxidized	2·02	
l. of oxygen consumed/g protein oxidized	0·88	
Calculated oxygen consumption	1·44 l/day	1·65 l/day
Evaporation rate	1·3 mg H_2O/ml CO_2 (Fig. 11)	1·3 mg H_2O/ml CO_2 (Fig. 9)
a. *Water gained:*	(g)	(g)
Preformed	0·17	0·20
Metabolic	0·93	1·07
Total	1·10	1·27
b. *Water lost:*		
Evaporation ($RQ = 0·71$)	1·33	1·52
Excreta	0·37	0·30
Total	1·70	1·82
a − b	−0·60	−0·55

* Assuming that it is the same as that of birds adjusted to water deprivation.

temperature 38°C or higher), these larks occasionally held their beaks open, and presumably were panting, when they stood in the sunshine. Usually, however, they sought shady places and remained inactive, which undoubtedly reduced their environmental and metabolic heat loads and minimized their need to thermoregulate by evaporation.

The Namib Desert, too, has quite moderate air temperatures, seldom over 40°C (Logan, 1960), and so these birds probably rarely need to increase evaporation when they remain inactive during the hottest time of day. Cade *et al.* (1965) found that the upper critical temperature of the zebra finch is as high as 42°C, and I have found a similarly high upper critical temperature in the silverbill *Lonchura malabarica*, a small xerophilous finch from northern Africa, Arabia and southern Asia (Willoughby, unpublished). In these species evaporative water loss is minimized up to these high upper critical temperatures because there is no increase in heat production up to that point, which otherwise would have to be lost by evaporation. It is tempting to hypothesize that the grey-backed finch-lark and Stark's lark have similarly high upper critical temperatures, and perhaps even undergo a limited hyperthermia at high ambient temperatures, so that the need to get rid of excess body heat by evaporation is minimized or obviated.

Probably the larks in the Namib need to use evaporative cooling only on a few days of the year; and they can probably replace the water they expend in this way by eating insects such as ants, termites and small beetles, which contain 60 per cent or more of water and are ubiquitous in the Namib, and bits of green vegetation. In any case, the unusually low rate of water exchange in these small birds reflects physiological adaptations to a dry environment.

SUMMARY

1. The Stark's lark and grey-backed finch-lark are two small (16–18 g) seed-eating birds that live in the very dry Namib Desert of South West Africa, and are independent of sources of drinking water there.

2. When deprived of drinking water and fed millet seed under moderate conditions of temperature and humidity, many individuals of both species could survive indefinitely and maintain body weight at a constant level after an initial weight loss during the first few days of deprivation.

3. The mean daily water consumption of 13 per cent and 8 per cent of body weight per bird for Stark's lark and grey-backed finch-lark, respectively, is lower than the predicted rate of evaporative water loss for birds of this size range in general.

4. The maximum concentration of NaCl that individuals of both species could drink and still maintain body weight was near 0·30 M.

5. Pulmo-cutaneous evaporation rates were low; and individual Stark's larks (but not grey-backed finch-larks) that had been deprived of water for 4 or 5 days had lower evaporation rates than individuals with water to drink. Evaporation rates for birds deprived of drinking water at ambient temperatures of 24–33°C averaged 3·5 mg/(g × hr) for both species.

6. Water content of feces and urine of water-deprived birds averaged about 51 per cent by weight in the grey-backed finch-lark, and 52 per cent in the Stark's lark.

7. A complete water budget for each species in the laboratory was constructed, and, on the average, daily water loss per bird exceeded water gain by about 0·6 g when birds consumed only air-dried seed; but water loss could be balanced against water gain in this budget by using water loss values near the lower end of the observed range.

8. The unusually low rates of water loss of these two species are adaptive to a dry environment.

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